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Progress Report

June 15, 1989 to June 14, 1992

Summary

This report covers work from June 15, 1989 to June 14, 1992. The main accomplishments have been: 1) Completion and publication of a comprehensive study of the effects of chromatic content, blur and contrast of targets on vernier acuity and on stereo acuity; 2) The use of a new method of measuring chromatic discrimination under conditions of constant adaptation and the publication of reports on this work; 3) Experiments on the significance of color in the perception of motion; 4) Experiments on the effects of chromatic adaptation on color matching; 5) The effects of noise masks on the detection of chromatic and luminance pulses; 6) Continuation of the study of the chromatic properties of single cells in the monkey cortex extending our experiments to Area V2; 7) Experiments on the effects on the responses of single neurons in monkey LGN to chromatic stimuli of chromatic adaptation; and 8) The development of a new system for making displays for visual experiments on TV monitors which allows at least 12 bits of accuracy in the specification of the intensity of each of the three primaries.

BACKGROUND

The main goal of our work is to understand the role of mechanisms operating at various levels in the visual system particularly the higher-order mechanisms in color vision. By higher-order mechanisms is meant those processes beyond the receptor level and beyond the conventionally-understood opponent color mechanisms.

Krauskopf, Williams and Heeley (1982), using an habituation procedure, found evidence for three sets of independent mechanisms selectively responsive to stimuli varying along three cardinal directions in color space. Two of these directions are chromatic and the third is a luminance axis. Following this, Derrington, Krauskopf and Lennie (1984) found two classes of parvocellular neurons in the monkey LGN, each maximally sensitive to modulation in time of uniform fields in one of the cardinal chromatic directions.

In subsequent research, Krauskopf, Williams, Mandler and Brown (1986) found psychophysical evidence for mechanisms selectively responsive to stimuli in other than the cardinal directions. Krauskopf, Zaidi and Mandler (1986) made measurements of simultaneous color contrast using a nulling technique and concluded that this phenomenon could not be explained in terms of the properties of receptor or second stage mechanisms. In electrophysiological experiments, Lennie, Krauskopf and Sclar (1990) have discovered some neurons in primary visual cortex (V1) of monkey that respond best to stimuli modulated along non-cardinal directions and thus may be part of a system of higher-order mechanisms.

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GENERAL METHODS

The results of Krauskopf, Williams and Heeley (1982) and Derrington, Krauskopf and Lennie (1984) have led us to use the color space depicted in Fig. 1. This space expresses the hypothesis that there are three independent mechanisms that respond to algebraic sums of the excitations of the three classes of cone photoreceptors. One of these responds to the difference between the excitations of the long wavelength sensitive (L) cone and the middle wavelength sensitive (M) cones and is called the L-M mechanism. The second responds to the difference between the short wavelength sensitive (S) cones on the one hand and the sum of the excitations of the L and M cones on the other and is called the S-(L+M) mechanism. The third mechanism responds to the sum of the excitations of the L and M cones and is called the Luminance mechanism.

The central point of this space is an equal-energy white. There are two chromatic axes which lie within the isoluminant plane through the white point. Along one of these axis the input to only the L-M mechanism varies. Along the second the input to only the S-(L+M) mechanism varies. Along the third axis only the input to the L+M mechanism varies.

These cardinal axes are similar but clearly different from the classical "opponent processes" in that while variation along the Constant B axis produces stimuli that appear reddish or greenish, variation along the Constant R&G axis produces stimuli that appear yellowish-green and purplish, not unique yellow and unique blue. Stimulus variation along the luminance axis results in changes in brightness with no change in hue.

All the stimuli in the experiments discussed here were generated on a television display driven under computer control using an Adage frame buffer system. This system allows linear control of the intensity of the three television primaries to nearly 10-bit accuracy. The spatial resolution is approximately one pixel per minute of visual angle.

Psychophysics of color vision

1) Offset Thresholds:

There has been a good deal of speculation recently on the properties of separate systems for the processing of stimuli defined by luminance variation ("luminance mechanisms") and stimuli defined by isoluminant chromatic variation ("chromatic mechanisms"). In particular it has been held that chromatic mechanisms are not as efficient as luminance mechanisms in processing spatial information (Livingston and Hubel, 1984; Morgan and Aiba, 1985). In order to test this notion a comprehensive set of experiments has been performed to examine the effects on vernier (offset) acuity of the chromatic content, blur and contrast of the test targets.

We have measured offset thresholds for targets with gaussian spatial profiles defined either by luminance or by chromatic contrast with respect to a neutral background. The tests were defined by excursions in each of the six cardinal directions. Thus they appeared "reddish", "yellowish", "greenish", "bluish" if isoluminant with the background or as luminance increments or decrements with respect to the equal-energy white background. The contrast of the targets was varied from the lowest level at which judgements could be made to the maximum contrast that could be achieved in that chromatic direction. The effect of blur was evaluated by varying the standard deviation of the gaussian profile.

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In order to decide whether chromatic mechanisms are less efficient at spatial discrimination than luminance mechanisms, it is necessary to equate the effective contrast of isoluminant and luminous stimuli. We did this by scaling the contrast of the targets used in the offset threshold experiments by their contrast thresholds. Thus, we plotted offset thresholds as a function of log contrast relative to contrast threshold for stimuli in each of six color directions.

If chromatic mechanisms were less efficient in processing spatial information than are luminance mechanisms, we would expect the offset thresholds for chromatic targets to plot above those for luminance targets. The overall impression from most of the results of this experiment is that offset thresholds vary markedly as a function of contrast and as a function of blur; but they are approximately the same for luminance and isoluminant stimuli of equal contrast and blur.

2) Chromatic discrimination and adaptation

We have continued to study the effects of chromatic adaptation on color discrimination. We have found, contrary to the previously accepted view, that the variation over color space of color discrimination follows very simple rules when care is taken to keep adaptation constant at the point in color space at which the discriminations are made. That these simple relations were not previously found can be understood from our findings that transient changes in adaptation profoundly effect color discrimination (Krauskopf, Williams and Heeley, 1982).

An important problem upon which these experiments have cast new light is where in the visual pathway do the processes underlying adaptation occur. One commonly held view is that the sensitivity of each class of cone receptors is regulated by the level of excitation of that class alone. Our experiments (Krauskopf and Gegenfurtner, 1990; and Krauskopf, Würger and Gegenfurtner, 1991) have shown that this explanation is neither necessary nor sufficient. On the one hand, we found that thresholds for the detection of pulses of light changing the input of the S cones only were elevated by increasing only the L and M cone excitation of the background showing that a change in the excitation of the S cones was not necessary to elevate the thresholds. On the other hand we found that thresholds for detecting changes along the L-M axis are constant failing to confirm the theory that the cone signals are of the form $\frac{\Delta M}{M}$ and $\frac{\Delta L}{L}$ which predicts that they should decrease when the relative contribution L cone input increases.

Color Discrimination under Constant Adaptation:

One of the central problems of color vision is how discrimination varies over color space. MacAdam (1942), in a classical experiment, had observers make color matches to a variety of stimuli using a method of adjustment. He used the standard deviation of the matches as a measure of discriminability. By using matching stimuli that varied in different directions about the standard stimuli he was able to construct equal-discriminability ellipses about points throughout the C.I.E. chromaticity chart. In MacAdam's procedure, the observer's adaptation level was determined by the standard stimulus and thus was different for each ellipse.

We were interested, for both theoretical and practical reasons, in measuring chromatic discrimination under conditions of constant adaptation. The observer's state of adaptation was controlled by viewing a uniform square 10 degrees on a side displayed on a television monitor. The stimulus pattern, consisted of three test (T) discs of one color and a fourth comparison (C) disc differed in some direction in color space from them. The observer's task was to identify the

location of the C disc which varied randomly from trial-to-trial. The threshold difference between the T and C stimuli was estimated by using a 3 to 1 staircase procedure.

Two regimes were studied. Under the first regime the observer was adapted to the region of color space in which the discriminations were made. Thresholds for detecting changes along the S-(L+M) axis are a linearly increasing function the excitation of the S cones. Thresholds for detecting changes along the L-M axis are independent of the locus of adaptation along this axis. The straightness of these functions is inconsistent with the theory that second stage mechanisms are more sensitive in the middle of their operating ranges. No convincing evidence of interactions in the effects of adaptation locus or test stimuli was observed.

Under the second regime the observer was adapted to one point in color space and the stimuli to be discriminated were located in other places in color space. Discrimination seems to be limited primarily by mechanisms maximally sensitive to modulation along the isoluminant cardinal axes but evidence suggestive of the operation of higher order mechanisms was also found.

3) The Influence of Color on the Perception of Coherent Motion

We completed a series of experiments on the role that chromatic mechanisms play in the perception of motion (Krauskopf and Farell, 1990). We obtained quite surprising results concerning the role played in the perception of motion by the mechanisms selectively responsive to modulation along the cardinal directions of color space. Drifting gratings modulated along different cardinal directions appear to slip with respect to one another. In contrast, when the directions of the modulations are rotated by 45 degrees, the gratings cohere. We conclude that information about movement is conveyed to a high level in the processing chain within mechanisms maximally responsive along the cardinal directions. The results contradict the notion that there exist separate mechanisms for the perception of color and motion. The results also argue against the idea that only the magnocellular pathway is significant in the perception of motion.

4) Color Appearance Changes Resulting from Chromatic Adaptation

Asymmetric color matches were obtained under conditions of steady-state chromatic adaptation to lights of equal luminance differing either in L-M (red and green) or in S cone excitation (yellowish and bluish) from the standard equal-energy achromatic adapting light. The changes in color appearance induced by the transition from a grey to a chromatic adapting light is a measure for the effect of chromatic adaptation on the color appearance of the briefly presented test lights.

We tested the following hypotheses. Our first and most general hypothesis is that the changes in color appearance induced by the transition from an achromatic standard adapting light to a chromatic adapting light can be described as a linear transformation in three-dimensional color space. Our second and more specific hypothesis is that the color appearance changes resulting from chromatic adaptation are predicted by a coefficient law in cone excitation space, i.e. the color appearance changes are predicted by scaling the cone signals of the test light. Our third hypothesis is that a strong coefficient law holds in the cardinal direction space (Krauskopf, Williams & Heeley, 1982), i.e. we asked whether adapting lights differing only in L-M cone excitation result in appearance changes which require adjustment along the L-M cone axis only. And conversely, we asked whether adapting lights differing in S cone excitation only induce color changes which require adjustment along the S cone axis only.

We obtained the following results. First, adapting lights differing in S cone excitation only from the standard adapting light produced nonlinearities. For adapting lights varying along the

L-M axis from the standard adapting light we did not find any deviations from linearity. Second, adapting lights differing in S cone excitation only from the standard adapting light produce color appearance changes which are inconsistent with a coefficient law, i.e. the color appearance changes of the test flash induced by yellowish and bluish adapting lights could not be accounted for by scaling the cone signals of the test light. For adapting lights varying along the L-M axis from the standard adapting light the results are compatible with a coefficient law, i.e. the color appearance changes resulting from red and green adaptation are predicted by scaling the cone excitations of the test light. However, the fact that adapting lights differing only in L-M cone excitation yield color appearance changes such that adjustment along the S cone direction is required, implies that the coefficients for at least two cone classes depend on the adapting input to the other cone classes. Third, the color appearance changes are inconsistent with a strong coefficient law in cardinal direction space. The color changes caused by adapting lights differing along the S cone axis only are not confined to this axis; similarly, adapting lights differing in L-M cone excitations produce appearance changes which require adjustment not only along the L-M cone axis but also along the S cone axis.

Furthermore, we found evidence that the adaptational effects, i.e. the induced color appearance changes, are not additive. Color appearance changes due to transition from grey to an adapting light differing in L-M as well as in S cone excitation (orange adapting light) could not be predicted by adding the color changes induced by adapting lights differing either along the L-M (red adapting light) or along the S cone axis (yellowish adapting light).

Electrophysiology of color vision

Collaborative electrophysiological research on color vision in Macaques with Peter Lennie of the University of Rochester continues. Our work which began with experiments on the lateral geniculate nucleus (Derrington, *et al.*, 1984) and was pursued further in the primary visual cortex (Lennie, *et al.*, 1990). Lennie, Krauskopf and Sclar (1990) have discovered some neurons in primary visual cortex (V1) of monkey that respond best to stimuli modulated along non-cardinal directions and thus may be part of a system of higher-order mechanisms. DePriest, Lennie and I (1991) have studied the effects of chromatic adaptation on the resting discharge and on the responses to chromatic pulses. These experiments relate directly to our psychophysical studies of chromatic discrimination. We have found that both the variability of the resting discharge and the amplitude of the responses to standard test stimuli vary with the locus of the adaptation field in color space in such a way to yield a constant signal-to-noise ratio. This surprising result is in accord with our psychophysical results which show that thresholds for discrimination along the "red-green" cardinal axis are invariant.

Programs were written and used in collaborative experiments with J. A. Movshon of N.Y.U. on the responses of neurons in macaque areas V1, V2 and MT to chromatic and achromatic moving stimuli. The patterns used include both simple and compound ("plaid") gratings. The experiments seek to identify the substrate for the results on the perception of such stimuli obtained by Krauskopf and Farell (1990) discussed above. These programs provide for the generation of stimuli on a color TV monitor using an Adage frame buffer controller. The 68000 processor, incorporated in the Adage, which runs the programs also is linked to the computer which runs the physiological aspects of the experiment (collecting spike counts and analyzing them). This computer is able efficiently to request the presentation of the stimuli required by passing parameters and a numerical code requesting the particular class of stimulus

needed.

Technology

We have used an NIH Small Instrumentation Program grant to build a new general purpose device for producing experimental stimuli on color TV monitors. The new system was designed and constructed by Walter Kropfl of our center who also has developed a new Postscript like interpreter for use in controlling experiments. The new system allows control of the intensity of each of the three primaries of the color TV monitor in theory to 16 bits of accuracy. We have written calibration and experimental programs for the new system. We have found that in fact the accuracy of control is at least to 12 bits, or four times better than the nominal accuracy of the best systems on the market.

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